

FINAL REPORT

PREDICTING THE ABILITY OF MARINE MAMMAL POPULATIONS TO COMPENSATE FOR BEHAVIORAL DISTURBANCES

David Lusseau
University of Aberdeen
Institute of Biological and Environmental Sciences
Tyllidrone Ave
Aberdeen, AB24 2TZ, UK.
phone: (+44) 1224-272843 fax: (+44) 1224-272396 email: d.lusseau@abdn.ac.uk

Award Number: N000141310696
<http://www.abdn.ac.uk/biologicalsci/staff/details/d.lusseau>

LONG-TERM GOALS

This project has aimed to develop predictive, analytical tools to help determine the ability of marine mammal populations to respond to behavioral disturbances. These tools are to be generic and applicable in a wide range of conditions, including scenarios where data might be limited. Building on recent advances in the field of behavioral ecology, we have focussed on defining the state resilience of behavioral strategies by considering the transient dynamics of these behavioral strategies, using systems of linear equations. The aim has been to provide a framework that allows an assessment of how probable it is that disturbance events lead to population scale consequences.

OBJECTIVES

- Develop simple, generic measures that allow the estimation of marine mammal populations and individuals to compensate for behavioral disturbances.
- Determining whether behavioral constraints can influence this resilience
- Testing these measures against real data from a data rich system
- Use simulations to infer resilience in data poor conditions

APPROACH

Measure of resilience and predictability exist for a variety of data sets [1]. This project aimed to introduce these measures to the study of animal behavior, using a variety of approaches, including simple theoretical models as well as statistical analysis of data rich conditions. Building on models developed for PCoD [2,3], we aimed to assess resilience of behavioral patterns for individuals in different ecological and life history conditions.

We analysed the stability of generic, linear system of ordinary differential equations (ODEs) across a wide range of parameter space for a simple model linking individual's behavior to their condition and

the ecological environment they are experiencing. We used simple measures of behavioral resilience that aim to capture both short and long term responses to behavioral disturbance.

We then used a previously developed model for northern elephant seals (*Mirounga angustirostris*) by Schick et al. [3] to assess the stability and transient dynamics of this behaviour-condition model. We parameterised this model for multiple individual seals from Año Nuevo in California, and then calculating the resilience measure we developed for each of the individual animals to predict which individuals would show the greatest response to disturbance.

Recent studies show that northern elephant seals from Año Nuevo have three different foraging tactics at sea [3]. Some individuals use the Northeast Pacific, while others remain in coastal waters and others again use the North Pacific Transition Zone (NPTZ). Yet, these individuals come from the same colony and therefore have very similar constraints placed on their behavior. Such inter-individual variability can be interpreted as different states of the northern elephant seal's behavior system. Data on these different foraging strategies were derived from an 8-year data set that is composed of measurements of over 300 adult female elephant seals. For these females the Costa Lab at UCSC has measured foraging trip duration, foraging location (i.e. coastal vs NPTZ), mass gain over the trip, body composition over the trip, reproductive parameters (pregnant or not pregnant), and whether the pup survived. Since we have multiple DTAG tracks of the same individual seals across years, we were able to compare individuals across seasons for a small subset of individuals repeatedly sampled. Considering El Nino climate events as a pressed disturbance, we predicted that seals with higher resilience measures would perform better during these long-term climate disturbances when compared to their behavior during a more typical year.

Finally, we have used the same data set to consider pulsed disturbance events. The Costa lab at UCSC's data set also includes dive profiles, from which it is possible to determine activity state (whether the individual is foraging, processing food or transiting through an area of ocean), and dive durations. Previous work by the Costa Lab shows that disturbed dives had a very different profile to others. We modelled the dive activity dynamics of individual seals to estimate dive activity transition probabilities before and after disturbance events. From those models we could predict dive activity resilience for seals and compare those to determine the effects of disturbance events.

WORK COMPLETED

All tasks are now completed. Details of technical approaches and main findings are provided below.

RESULTS

Analysis of a simple model to test predictions from developed measures

Following peer-review of this section of the work, we have now expanded the system of equations to include population dynamics [5]. This provides an important approach to assess under which system conditions is population trajectory most likely to be affected (the central aim of PCoD).

For the revised model presented here, we include a population size variable N in the system of differential equations, to allow us to consider how density dependent interactions will affect the calculation of resilience. Note that in this instance the condition and feeding rate parameters are considered as population averages, rather than measures of a specific individual. The model is then:

$$\begin{pmatrix} \frac{dF}{dt} \\ \frac{dC}{dt} \\ \frac{dE}{dt} \\ \frac{dN}{dt} \end{pmatrix} = \begin{pmatrix} -a_1 & -a_2 & a_3 & 0 \\ \frac{b_1 F}{1+b_1 F} & -b_2 & 0 & \frac{1-b_3 N}{b_3} \\ -c_1 N & 0 & c_3 & 0 \\ 0 & d_2 & 0 & d_4(d_3 E - N) \end{pmatrix} \begin{pmatrix} F \\ C \\ E \\ N \end{pmatrix} \quad [\text{Eq. 1}]$$

where F is the averaged feeding rate of individuals, C is the averaged condition individuals (here used as a proxy for individual health as defined in PCoD), and E is the quality of the environment in which the individuals finds itself. Environment quality can be interpreted as resource richness, ensuring that low quality environments reduce the feeding rate of an individual when compared to higher quality environments. The parameter a_3 indicates how much feeding increases with an improvement in resource availability. Parameter a_2 is the scale at which well-conditioned animals will scale back their feeding, whether for physiological reasons. a_1 indicates damping on the feeding rate itself - as an individual must also perform other activities, a high feeding rate is unsustainable, so when the current feeding rate is high the individual will slow down, while low current rates will drive the individual to increase the time spend foraging. Larger a_1 will increase the non-feeding demands of an individual, resulting in a larger decrease in feeding rate when it has previously been high. Parameter b_1 can be considered as the feeding efficiency of an individual, determining how well food intake is translated into improved condition, while parameter b_2 indicates that positive condition will decline with time when no food is added, and can thus be interpreted as a measure of metabolism speed. Feeding rates will reduce the abundance of resources in the environment, and c_1 indicates how quickly this will occur. The higher c_1 is, the more efficient a forager the individual is, and therefore the larger the decrease in environmental quality for a fixed feeding rate. Finally, c_3 indicates that the environment, in the absence of the considered individuals, will find a fixed value (such as the carrying capacity of a prey item). Therefore, in the absence of feeding pressure environments with higher resources or quality will decline, and low quality environments will increase. Higher values of c_3 indicate faster reversion to this fixed value.

The parameter d_2 indicates that a group with high average condition will be expected to have greater survivorship and reproductive output, and therefore the population N will grow faster. The population size at which density dependence becomes detrimental is determined by d_3 , with the carrying capacity of an environment with quality E given by $d_3 E$, while d_4 determines the strength of the density dependent effects, with a higher d_4 ensuring density dependent effects are stronger. Note that high population will lead to reductions in condition as competition increases (b_3).

We simulated 1,000,000 systems drawing randomly values for each parameters each time. The values for a_i, b_i , and c_i were drawn from a uniform distribution over the interval $[0,1]$. The values of the parameters d_i were drawn from a uniform distribution over the interval $[0,0.01]$, two orders of magnitude smaller than the other parameters, to indicate the slower time scale changes in population occur over.

Mathematically, resilience can be calculated from the Jacobian of a this PCoD model, the matrix of partial derivatives of the model, which is determined by the model parameters. Resilience, formally ‘engineering resilience’, is given by the maximum absolute value of the real parts of the Jacobian’s eigenvalues, $\max_i |\text{Re}(\lambda_i)|$ where λ_i is the i -th eigenvalue of the Jacobian \mathbf{J} . We can also used the eigenvalues of \mathbf{J} to determine the type of state in which each of the simulated was; particularly whether

it was a stable state, such as attractive nodes or foci, or an unstable state (repulsive nodes and foci, or saddles). This qualification of the state allows us to determine the transient dynamics of the systems around equilibrium. This is important as this determines the behavior the system will have when perturbed from equilibrium (after a disturbance): unstable systems will be pushed away from equilibrium while stable systems will be more likely to recover. The resilience (measured as stated above) of the system will determine the effect of a perturbation; in other word in our system (Eq. 1), the population consequences of disturbances.

Of the 1,000,000 simulated systems, 310,797 were stable; 3,516 attractive nodes and 307,281 attractive foci (Figure 1 presents the coordinate of those equilibria along the 4 dimensions of the system). Stable systems, unsurprisingly were significantly more resilient than unstable systems (see annual report, FY14).

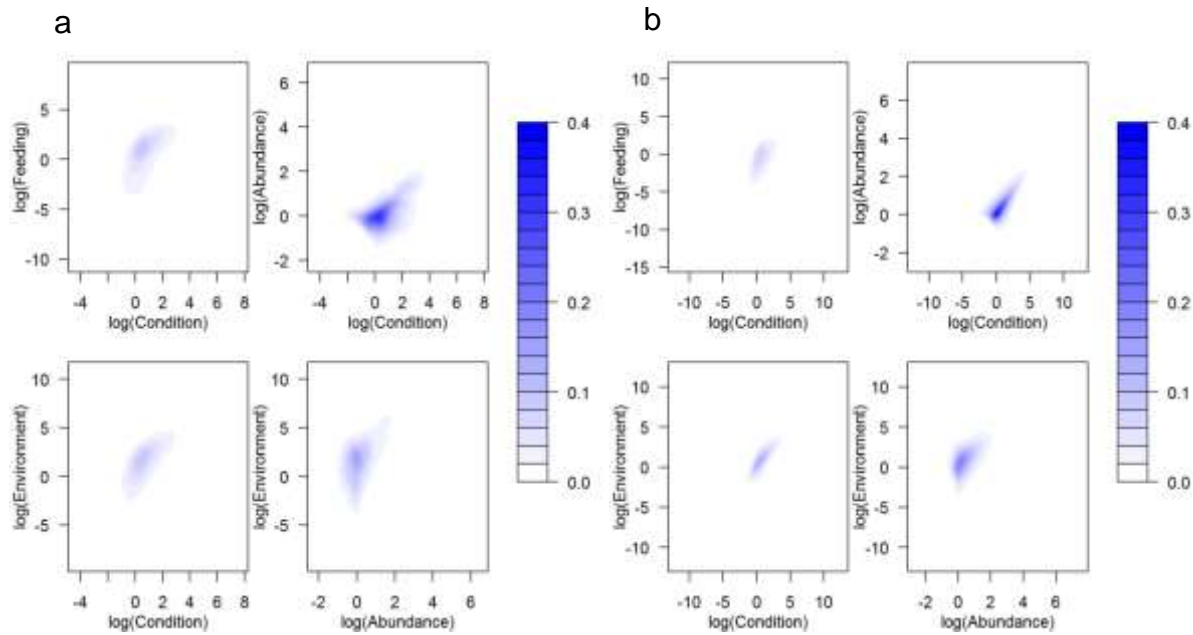


Figure 1. Conditional density distribution of equilibria for stable states (attractive nodes, $n= 3516$, and attractive foci, $n=307281$); color intensity corresponds to the density of those stable states.

These simulations showed that key system parameters differed between stable equilibrium types. Of particular interest is the relationship between feeding rate of change (a_1) and condition rate of change (b_2). These change along the axis of capital-income breeding strategies, with capital breeders having a slow condition rate of change and a higher feeding rate of change; while income breeders tend to have a faster condition rate of change. Attractive nodes seem to assort themselves into two groups along this axis (Figure 2a), while attractive foci did not (Figure 2b).

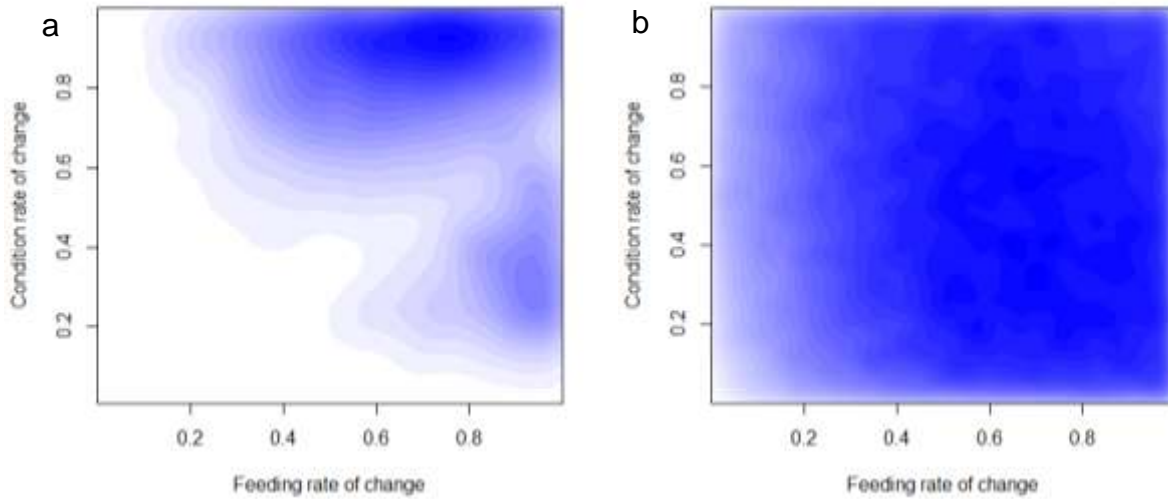


Figure 2. *Estimated condition (b_2) and feeding (a_1) rate of change for attractive nodes (a) and foci (b).*

We fitted generalised linear models to assess which system parameters most influenced whether a system was stable or not. Environmental dynamics is crucial to stability, with stability increasing with a decrease in environmental recovery rate (c_3 , Figure 3). The consumption rate (c_1) interacts with this effect, increasing stability for low environmental recovery rates (Figure 3).

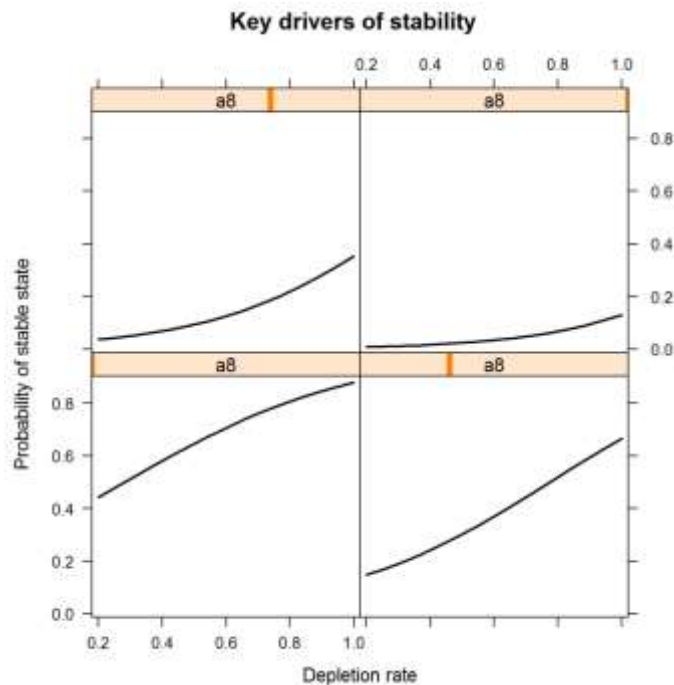


Figure 3. *Key parameters of the system influencing whether an equilibrium is stable (attractive node or focus) or not. The rates at which individuals consume the environment (depletion rate, c_1) and the environment replenishes itself (c_3 , here labelled a_8) interact to influence the emergence of stability. Predicted values from a fitted generalised linear model (binomial errors).*

For all stable systems, the condition rate of change (b_2) influences the resilience of the systems (Figure 4). In other words, the slower the rate at which an individual's condition changes the more resilient it is. So we expect life history strategies selecting for slow change in condition to be more resilient to perturbations.

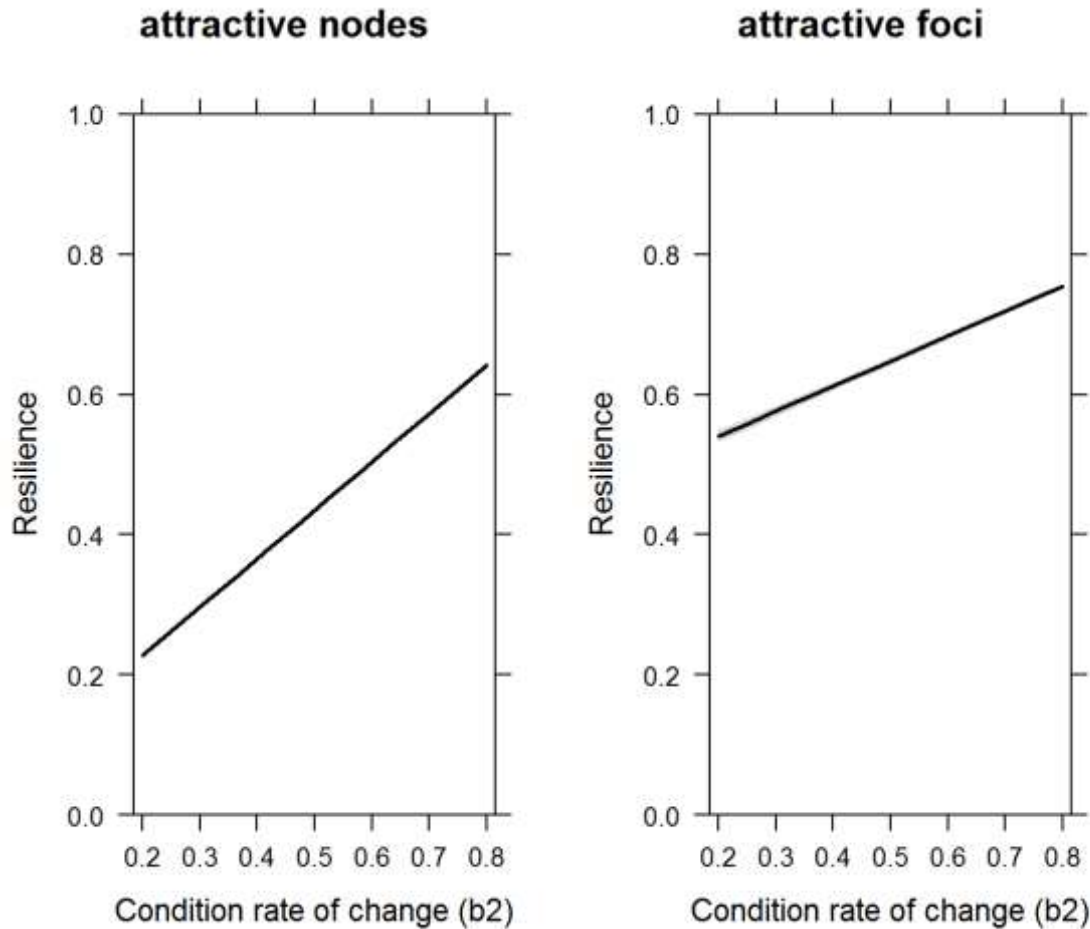


Figure 4. The influence of condition rate of change (b_2 Eq. 1) on system's engineering resilience. Predicted value from a fitted general linear model, including 95% confidence interval (grey band).

Preliminary conclusions emerging from the system simulations

Two main conclusions are emerging from this simulation work. Firstly, the dynamics of the environment in which populations live is a key factor in stability; environment that change slowly are more likely to confer the foundations for stable systems. Those environment are more likely to provide the mean for population to recover from perturbations. Secondly, The resilience of those populations to perturbations, which encompasses both the magnitude of the perturbation's effect as well as the time it will take a population to recover, will depend on the rate at which the condition of individuals will change. Slow condition change will increase the resilience of the populations. The transient dynamics around the equilibria will affect resilience as well, attractive node are less resilient than attractive foci.

Prediction of the effect of perturbations on simulated systems

This work provides predictions for the way each of those 1,000,000 systems should respond to perturbations. We simulated an environmental perturbation by decreasing the value of E for each stable

systems by 10%. We then tracked the magnitude of the effect this environmental perturbation had on the population abundance as well as the time it took the population abundance to recover to the stable N.

The environmental perturbation had less of an effect on more resilient attractive foci systems ($F_{1,306292}=267.88$, $p<0.0001$, Figure 5a) and more resilient attractive node systems ($F_{1,3511}=9.45$, $p=0.002$, Figure 5b).

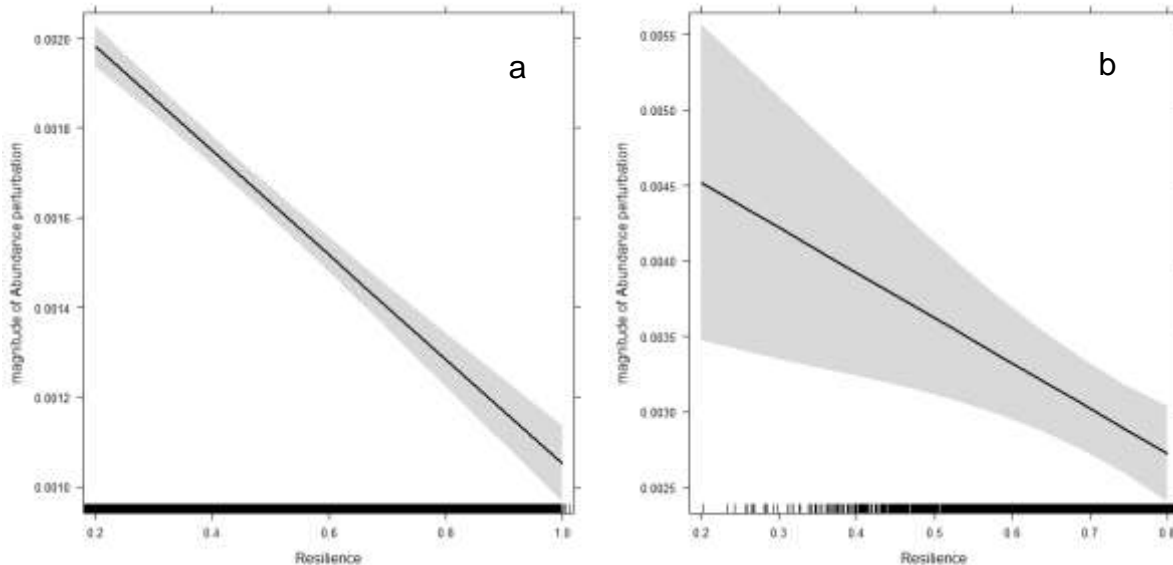


Figure 5. Predicted effect of resilience on the magnitude of abundance change in response to an environmental perturbation, grey band is 95% confidence interval, for attractive foci (a) and node (b). Note, the difference in the y-axes of the plots, on average nodes were more perturbed than foci.

However, the system resilience did not predict the time it took abundance to recover from the perturbation. This system-level resilience measure was not a good proxy for variable-level predictions on recovery time.

Using measures of resilience to predict changes after perturbations in real-world scenarios

We presented in the previous annual report the study of pressed perturbations (El Niño events) on elephant seals. This showed that more resilient individuals, defined in the same way as we did in our simulation work, tend to indeed be more ‘resilient’ to pressed perturbations, as they tended to be able to retain similar mass gains over their foraging trip during an ElNiño event compared to ‘normal’ ecological conditions. However sample size (requiring instrumentation of the same seals in multiple years) was small to make strong inferences, beyond describing this tendency.

We can also detect pulsed disturbances of northern elephant seals from their dive tracks. Dives that are longer than 5000 seconds have previously been described as identifiers for a disturbance event. We detected 31 such events in the tracks available. As the dive activity budget is not stable over the duration of the foraging trip [3], the resilience of seals to pulsed perturbations will depend on the timing of that event. A time-continuous multi-state model (markovian model) was fitted to the dive type time series for each track for a 2-week period prior to the disturbances. Average dive time was used to estimate the dive category transition probability matrix (tpm) for each 2-week period. The

damping ratio was estimated as a measure of resilience from this tpm as previously described in an ecological context [6]. The tpm damping ratio was estimated from ratio the first to the second eigenvalue of the tpm, leading engineering resilience to be $\ln(\frac{\lambda_1}{|\lambda_2|})$ [6].

This provided us with a prediction of the resilience of a seal's diving activities prior to a perturbation. Once the perturbation occurred (dive time > 5000sec), we estimated the magnitude of the perturbation as the dive time and the time it took the seal to recover to a stable dive activity pattern. To do so, we estimated the cumulative proportion of time spent in each dive type using dive as a step over the next 1000 dives, so that we obtained 1000 diving activity budget, one estimated at each dive. This cumulative dive budget should "stabilise" as we move away from the disturbance. We fitted Bayesian multivariate change point models (library bcp, 7) to determine when the variance across all dive types stabilised over these 1000 dive steps. This point corresponds to when the disturbance effect stopped affecting the dive budget.

As expected, more resilient seals recovered faster from a perturbation ($F_{1,29} = 5.0$, $p = 0.03$, Figure 6a). The dive duration during the perturbation was longer for more resilient seals ($F_{1,29} = 8.0$, $p = 0.008$, Figure 6b). This provides a demonstration of the importance of the context in which resilience is interpreted. Here we measured the resilience of dive activities and measured disturbance effect as dive duration. The increased dive duration is interpreted as an evasive tactic, hence here more resilient seals are able to evade a perceived risk for longer than others. Resilience conferred two advantages to seals: a quicker recovery to normal diving activities, and a greater flexibility to engage in response to risk.

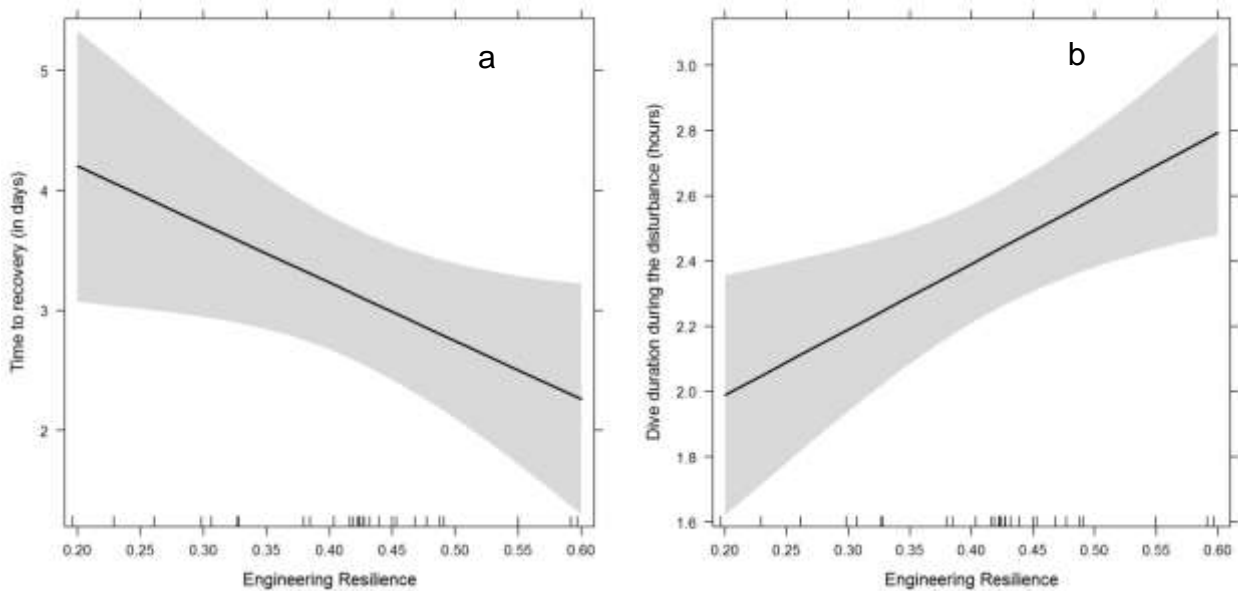


Figure 6. Predicted effect of seal dive activity resilience on (a) the time it took seals to recover from a perturbation and (b) the dive duration of seals during the perturbation. Prediction from fitted linear models, grey band is 95% confidence interval.

IMPACT/APPLICATIONS

This project instigated the development of Predictive Analytical Tools for the Rapid Assessment of Population Consequences of Disturbances (PATRA for PCOD). A direct application of this study is

the understanding that measuring behaviour and health prior to a planned perturbation can provide an indication of the propensity that a disturbance will have a long-lasting impact or not on the animals affected. This will be a factor of the species that is perturbed and the ecological conditions at the time. We can estimate resilience measure from behavioural and physiological time series. Those measure will provide an estimate of how quickly perturbed animals will recover from a disturbance and the magnitude of the impact of this diturbance.

This project also provide a rapid assessment tool to categorise populations that are likely to be more at risk of PCoD. Firstly, we show that environmental dynamics influence the stability of behavior-condition-population systems, with slower environments conferring a greater propensity for stability. In stable systems, the rate of change in animal condition influenced their resilience, with species for which condition changes slowly being more resilient. This resilience diminishes the impact of a perturbation. However, this system-level measure of resilience does not provide with an estimate of how fast a population will recover from a perturbation; for this we need a variable-specific measure of resilience.

TRANSITIONS

Two avenues are now opened. First, we can now rank population resilience to perturbations based on the environment in which they live and the species physiological traits. This exercise would provide a matrix to assess species/location priorities for PCoD appraisal. Second, we need to further groundproof behavioural and physiological-specific measures of resilience for a wider array of species.

RELATED PROJECTS

[NONE]

REFERENCES

1. van Nes, E. H. & Scheffer, M. Slow recovery from perturbations as a generic indicator of a nearby catastrophic shift. *American Naturalist* 169, 738-747 (2007).
2. New L.F., et al. Modelling the biological significance of behavioural change in coastal bottlenose dolphins in response to disturbance. *Functional Ecology* 27, 314-322 (2013).
3. Schick, R. S. et al. Estimating resource acquisition and at-sea body condition of a marine predator. *Journal of Animal Ecology*, 82: 1300-1315 (2013).
4. Vasseur D.A. and Yodzis P. The color of environmental noise. *Ecology* 85, 1146-1152 (2004)
5. Natrass S. & Lusseau D. Using resilience to predict the effects of disturbance. *Scientific Reports* (revised)
6. Wootton J.T. Markov hain models predict the consequences of experimental extinctions. *Ecology Letters* 7: 653-660. (2004).
7. Erdman C & Emerson J.W. bcp: An R Package for Performing a Bayesian Analysis of Change Point Problems, *Journal of Statistical Software* 23: 1-13. (2007)

PUBLICATIONS

Natrass S. & Lusseau D. (revised). Using resilience to predict the effects of disturbance. *Scientific Reports*

Presentations

Nattrass S. 2014. Analytic measures for predicting population consequences of disturbance. Annual Meeting of the Society for Mathematical Biology and Japanese Society for Mathematical Biology: Osaka, Japan

Nattrass S. 2014. Analytic measures for predicting population consequences of disturbance. Animal Behavior Society Meeting: Princeton, NJ.

Nattrass S. 2014. The effects of behavioural disturbance on population dynamics in capital breeders. Models in Population Dynamics and Ecology: Turin, Italy.